

## DEFENSIVE CHEMISTRY OF AN APOSEMATIC BUG, *Pachycoris stallii* UHLER AND VOLATILE COMPOUNDS OF ITS HOST PLANT *Croton californicus* MUELL.-ARG.

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**Abstract**—Volatile components of *Pachycoris stallii* scent gland secretions and the bug's host plant, *Croton californicus*, were identified by gas chromatography and mass spectroscopy. The predominant compounds isolated from *C. californicus* fruit and leaves were  $\beta$ -myrcene and  $\beta$ -caryophyllene. Metathoracic gland secretions of *P. stallii* contained mostly (*E*)-2-hexenal, (*E*)-4-oxo-2-hexenal, (*E*)-2-hexenyl acetate, and *n*-tridecane. In males, *n*-tridecane was present throughout the metathoracic gland, but in females this compound was found only in the median reservoir/accessory gland. (*E*)-2-Hexenal was present throughout the gland of female bugs, but in males was primarily present in the median reservoir/accessory gland. (*E*)-4-Oxo-2-hexenal and *n*-dodecane were isolated from the median reservoir/accessory gland of male and female bugs. Metathoracic glands were sexually monomorphic. Data from chemical analyses and anatomical observations suggest that dorsal abdominal glands of adults were apparently obsolescent. In nymphs, dorsal abdominal glands produced (*E*)-2-hexenal, (*E*)-4-oxo-2-hexenal, *n*-dodecane, *n*-tridecane, and tetradecanal. The proportion of the predominant constituent, (*E*)-4-oxo-2-hexenal, decreased from 72% in the first instar to 47% in the fourth instar. Proportions of tetradecanal and *n*-tridecane were greater in the fourth instar than in the first instar. Observations of dissected glands indicated that median and posterior dorsal abdominal glands of all nymphal instars were more developed than anterior dorsal abdominal glands. Scanning electron micrography revealed the presence of polygonal microsculpturing on the integument surrounding the ostioles of metathoracic and dorsal abdominal glands. Chemical, anatomical,

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and behavioral data indicated that *P. stallii* has a chemical defense system based on short-chain carbonyl compounds and that this system is directed against arthropods. The abundance of arthropod natural enemies apparently has forced *P. stallii* to maintain this defense system despite feeding on a toxic host plant.

**Key Words**—*Pachycoris stallii*, Pentatomoidea, Scutelleridae, allomone, *Croton californicus*, Euphorbiaceae, terpenoids, exocrine glands, aposematic, carbonyl defense.

## INTRODUCTION

Heteroptera are well-known for their chemical defense systems (Aldrich, 1988). Heteropteran allomones are typically produced in and expelled from: (1) adult metathoracic glands located ventrally in the metathorax and with lateral ostia between the meso- and metathoracic legs, and (2) adult and nymphal dorsal abdominal glands arranged in a metameric series of up to four dorsally located glands on abdominal tergites III to VI (Staddon, 1979; Aldrich, 1988, 1995). The defensive secretions are usually mixtures of unbranched aliphatic compounds, most with carbon chains of C<sub>6</sub>, C<sub>8</sub>, and C<sub>4</sub>, as well as some aromatic compounds (Staddon, 1979; Aldrich, 1995). These chemicals function as nonspecific toxins, irritants, and repellents, and are generally more effective against arthropods than birds or mammals (Eisner, 1970; Blum, 1981).

Aposematic heteropterans, like other apparent insects, have a high likelihood of discovery by natural enemies and are thus expected to be chemically well-defended (Pasteels et al., 1983). Aposematic bugs sometimes sequester compounds that are toxic to predators from host plants (Duffey and Scudder, 1972; Aldrich, 1988; Aldrich et al., 1996), or produce the typical allomones de novo or from simple precursors (Blum, 1981; Staddon et al., 1987; Krall et al., 1999). In many cases, sequestration of host toxins relaxes the selection pressure for production of typical exocrine gland secretions (Staddon et al., 1987; Aldrich, 1995; Aldrich et al., 1996).

*Pachycoris stallii* Uhler is an aposematic scutellerid bug of neotropical distribution. Adults are ca. 12 mm in length and are brown-black with 22 orange spots on the dorsum that sometimes coalesce. Nymphs are red with metallic blue-green markings on the abdomen, pronotum, head, and legs. *Pachycoris stallii* appears to be highly host specific to the euphorb *Croton californicus* Muell.-Arg. (Williams, unpublished observations), a perennial shrub that occurs in the southwestern United States and northwestern Mexico (Shreve and Wiggins, 1964). *Pachycoris stallii* is also a subsocial insect. Females oviposit on *C. californicus* leaves and guard the egg masses and first-instar nymphs from natural enemies (Williams, unpublished observations). With the exception of

first-instar nymphs that do not feed, all nymphal instars as well as adults feed on *C. californicus* seeds developing within capsular fruit. Early instar nymphs occur in aggregations on *C. californicus*. Field observations suggest that arthropods are the predominant natural enemies of *P. stallii* (Williams, unpublished observations). Like many Euphorbiaceae, *Croton* species produce an abundance of chemicals toxic and irritating to vertebrates (Upadhyay and Hecker, 1976; Chavez et al., 1982; Alexander et al., 1991). Phytochemicals in *C. californicus* apparently render it unpalatable, because herbivores, vertebrate and invertebrate alike, generally avoid it.

*Pachycoris stallii* is an aposematic insect that is relatively large and long-lived, apparently monophagous on a toxic host plant, and lives in aggregations in open habitat where it is attacked by other arthropods. Ecological theory predicts that such an insect should possess a fortified chemical defense system (Pasteels et al., 1983). The objectives of this study were to: (1) test the hypothesis that despite feeding on a toxic host plant that may confer protection against vertebrate predators, *P. stallii* maintains a potent exocrine gland defensive system directed at arthropods, and (2) describe the volatiles produced by *C. californicus*.

#### METHODS AND MATERIALS

*Preparation of Chemical Extracts.* *Croton californicus* and *P. stallii* were field-collected in Baja California, Mexico. Immediately after collection, three to seven *Croton* fruit or leaves were placed in a glass vial containing 1 ml ethyl acetate for 2 min, after which all plant tissue was removed and the vial was sealed.

*Pachycoris stallii* were held in plastic vials with several fresh *Croton* leaves until collection of secretions (<4 hr after collection). Metathoracic gland secretions were obtained from living bugs by two methods: dissection of whole glands and collection of rinsates from whole bugs. Whole glands were dissected in a paraffin-coated Petri dish with tap water and were separated into two groups: (1) median reservoirs with accessory glands (MR/AG) and (2) lateral reservoirs with secretory tubules (LR/ST). Excess water was drawn from the glands with tissue paper, after which the glands were placed in a glass vial with 0.5 ml ethyl acetate and macerated with a capillary tube. Whole-bug rinsates were collected by placing one to four adults of the same gender (females guarding egg masses, females not guarding egg masses, and males) into a glass vial with 1 ml ethyl acetate for 3 min, after which adults were removed. (Preliminary analyses indicated that dorsal abdominal glands of adult *P. stallii* produce only trace amounts of volatiles; thus, we attribute results from whole-bug rinses solely to metathoracic glands). Samples from one to six bugs were pooled for analysis.

Dorsal abdominal gland secretions were obtained from adults by dissection similar to that described for metathoracic glands. Anterior (tergites III–IV),

median (tergites IV–V), and posterior (tergites V–VI) dorsal abdominal glands were dissected separately. Samples from three to six bugs were pooled and stored in 0.5 ml ethyl acetate for analysis. Nymphal dorsal abdominal gland secretions were collected by placing 5–40 nymphs of the same instar in a glass vial with 1 ml ethyl acetate for 3 min, after which nymphs were removed. All extracts were held at  $-20^{\circ}\text{C}$  until chemical analysis.

*Chemical Analysis.* Extracts were analyzed on a Hewlett-Packard 5890 gas chromatograph with a 15-m  $\times$  0.32-mm-ID column coated with 0.25  $\mu\text{m}$  DB-5 film (J & W Scientific, Folsom, California) and equipped with a flame ionization detector. The injector temperature was  $200^{\circ}\text{C}$  and the detector temperature was  $240^{\circ}\text{C}$ . The temperature was held at  $60^{\circ}\text{C}$  for 1 min then increased at  $10^{\circ}\text{C}/\text{min}$  to  $220^{\circ}\text{C}$  and held for 4 min. Nitrogen (20 cm/sec) was used as the carrier gas.

Gas chromatographic–mass spectrometric (GC-MS) analyses were conducted on a Hewlett-Packard 5890 gas chromatograph and a 5970 mass spectrometer. Data were obtained by using a 25-m  $\times$  0.32-mm-ID column coated with 0.25  $\mu\text{m}$  film of DB-5 MS (J & W Scientific). The injector temperature was  $250^{\circ}\text{C}$  and the detector temperature was  $280^{\circ}\text{C}$ . The column temperature was held at  $60^{\circ}\text{C}$  for 2 min, then programmed at  $10^{\circ}\text{C}/\text{min}$  to  $230^{\circ}\text{C}$  and held for 2 min. The helium flow rate was 28.7 cm/sec. Electron impact (EI) mass spectra were measured at 70 eV.

GC-MS data were analyzed on a Hewlett-Packard ChemStation by using a NBS mass spectral library. Compounds were identified by comparison of the obtained mass spectra to library spectra and spectra of known standards, and by matching the obtained chromatographic retention times to those of known standard compounds.

*Gland Anatomy.* *Pachycoris stallii* adults and all five nymphal instars were killed and preserved in 70% ethanol. These bugs were dissected and observed with a dissecting scope to obtain gross morphological descriptions of metathoracic and dorsal abdominal glands. Scanning electron microscopy was used to study the efferent systems of metathoracic and dorsal abdominal glands. Specimens killed in 70% ethanol were sonicated for 1 min to remove debris, then passed through a graded ethanol series for dehydration, after which they were critical-point dried with carbon dioxide. Specimens were then mounted on SEM stubs using conductive silver paint, and were ion sputter-coated with gold before viewing with a Philips 501 scanning electron microscope (3.6–7.2 kV).

*Behavior of P. stallii.* Field observations of *P. stallii* behavior aided interpretation of the chemical and anatomical data.

## RESULTS

*Plant Chemistry.* GC-MS analysis showed that two compounds,  $\beta$ -myrcene and  $\beta$ -caryophyllene, were the major constituents in extracts of *C. californicus*

TABLE 1. COMPOUNDS PRESENT IN *Croton californicus*

Retention time (min)	Compound	Composition (%) <sup>a</sup>	
		Fruit	Leaves
6.19	3-thujene	2	3
7.21	$\beta$ -pinene	2	0
7.32	$\beta$ -myrcene	58	46
8.62	$\delta$ -terpinene	3	4
9.96	Unidentified	0	3
11.47	<i>n</i> -tridecane	2	5
14.63	$\beta$ -caryophyllene	23	30
15.14	$\alpha$ -caryophyllene	3	0
15.47	Unidentified sesquiterpene	7	5

<sup>a</sup>Percentages based on total ion area.

(Table 1). Together these terpenoids comprised at least 75% of the volatile compounds identified in fruit and leaves. Small quantities of other terpenoids and an unbranched aliphatic compound were also identified.

**Metathoracic Gland Chemistry.** The predominant secretory components identified in rinsates of adult *P. stalii* were (*E*)-2-hexenal, (*E*)-4-oxo-2-hexenal, (*E*)-2-hexenyl acetate, and *n*-tridecane (Table 2). Small quantities of unbranched aliphatic compounds were also present in rinsates of both genders. Aside from males having a greater proportion of (*E*)-2-hexenyl acetate than females, major differences in the relative proportions of chemical constituents were not observed between the genders (Table 2). In females, the most abundant constituents, in order of greatest proportion, were *n*-tridecane, (*E*)-2-hexenal, and (*E*)-4-oxo-2-hexenal. Together these compounds made up approximately 90% of the total volatiles collected from female metathoracic glands. In males, the most abundant constituents, in order of greatest proportion, were *n*-tridecane, (*E*)-2-hexenyl acetate, (*E*)-2-hexenal, and (*E*)-4-oxo-2-hexenal. These constituents comprised 96% of the total volatiles in male metathoracic glands. A possible explanation for the greater relative abundance of (*E*)-2-hexenyl acetate in male glands than in female glands may be that at the time the rinse was made some male bugs in the sample had not converted as much of the ester to the aldehyde as females had.

Results of chemical analyses of dissected metathoracic glands are presented in Table 3. Major differences were not observed in the chemical composition of metathoracic glands between females guarding egg masses and females not guarding egg masses. However, metathoracic gland secretions of males appeared to have a greater proportion of *n*-tridecane than was observed in females. In males, *n*-tridecane was present in MR/AG and LR/ST, but in females this compound was found only in MR/AG. (*E*)-2-Hexenal was present in both MR/AG

TABLE 2. COMPOUNDS PRESENT IN WHOLE-BUG RINSATES OF ADULT *Pachycoris stallii*

Retention time (min)	Compound	Composition (%) <sup>a</sup>		
		Female guarding egg mass	Female not guarding egg mass	Male
3.95	(E)-2-hexenal	32	36	20
5.85	(E)-4-oxo-2-hexenal	19	15	11
6.84	(E)-2-hexenyl acetate	4	trace	21
8.28	<i>n</i> -undecane	1	0	0
9.97	<i>n</i> -dodecane	4	3	2
11.42	1-tridecene	1	1	1
11.61	<i>n</i> -tridecane	38	44	44
13.00	<i>n</i> -tetradecane	trace	trace	0
14.38	<i>n</i> -pentadecane	1	trace	1

<sup>a</sup>Percentages based on GC peak areas.

and LR/ST of female bugs, but in males was primarily present in the MR/AG. (E)-4-Oxo-2-hexenal and *n*-dodecane were isolated from the MR/AG of male and female bugs.

**Dorsal Abdominal Gland Chemistry.** No volatiles were isolated from dorsal abdominal glands of adult female *P. stallii*. Adult males produced trace amounts of *n*-tridecane in the anterior and median dorsal abdominal glands, but no volatiles were isolated from posterior dorsal abdominal glands. Table 4 presents the volatile components identified from dorsal abdominal glands of first through fourth nymphal instar *P. stallii*. Rinsates of nymphs revealed the presence of (E)-2-hexenal, (E)-4-oxo-2-hexenal, *n*-dodecane, *n*-tridecane, and tetradecanal. Of these compounds, (E)-4-oxo-2-hexenal comprised the greatest proportion of total constituents in the four nymphal instars tested (Table 4). The proportion of (E)-4-oxo-2-hexenal decreased from 72% in the first instar to 47% in the fourth instar. Tetradecanal and *n*-tridecane were present in similar proportions in all instars except the second, and relative proportions of both compounds were greater in the fourth instar than in the first instar.

**Gland Anatomy.** Metathoracic glands of *P. stallii* were sexually monomorphic. Median reservoirs were bright orange, while lateral reservoirs were translucent and without pigment. Microsculpturing of the integument was present surrounding the metathoracic gland ostia on the mesepisternum and metepisternum (Figure 1). Ostioles of adult anterior dorsal abdominal glands were of the type 1 (undivided ostiole) described by Remold (1962), while median and posterior ostioles were of a gradient between types 1 and 2 (divided ostiole). Adult dorsal abdominal glands were small and apparently obsolescent. These glands were mostly translucent, but with a bit of orange pigment. Anterior dorsal abdominal glands were divided half-glands and were spherical, while median and posterior

TABLE 3. COMPOUNDS OBTAINED FROM DISSECTION OF *Pachycoris stallii* METATHORACIC GLANDS

Retention time (min)	Compound	Composition (%) <sup>a</sup>					
		Female guarding egg mass		Female not guarding egg mass		Male	
		MR/AG <sup>b</sup>	LR/ST <sup>c</sup>	MR/AG <sup>b</sup>	LR/ST <sup>c</sup>	MR/AG <sup>b</sup>	LR/ST <sup>c</sup>
2.76	( <i>E</i> )-2-hexenal	31	100	43	100	18	trace
3.92	( <i>E</i> )-4-oxo-2-hexenal	4	0	5	0	3	trace
4.75	( <i>E</i> )-2-hexenyl acetate	1	0	0	0	1	0
7.52	<i>n</i> -dodecane	1	0	0	0	1	0
8.98	<i>n</i> -tridecane	63	0	52	0	77	99

<sup>a</sup>Percentages based on GC peak areas.<sup>b</sup>Median reservoir and accessory gland.<sup>c</sup>Lateral reservoir and secretory tubules.

TABLE 4. COMPOUNDS PRESENT IN FIRST THROUGH FOURTH NYMPHAL INSTARS OF *Pachycoris stallii* DORSAL ABDOMINAL GLANDS

Retention time (min)	Compound	Composition (%) <sup>a</sup>			
		First instar	Second instar	Third instar	Fourth instar
2.71	( <i>E</i> )-2-hexenal	5	1	3	5
3.94	( <i>E</i> )-4-oxo-2-hexenal	72	61	52	47
7.51	<i>n</i> -dodecane	0	1	0	1
8.99	<i>n</i> -tridecane	12	23	22	22
13.15	tetradecanal	11	14	23	25

<sup>a</sup>Percentages based on GC peak areas.

glands were undivided and elongate. All five nymphal instars possessed ostioles of a similar arrangement as adults (anterior, type 1; median and posterior, type 2) (Figure 2). Anterior dorsal abdominal glands of all nymphal instars resembled those of adults in relative size, shape, and color. Compared to the anterior glands, median and posterior dorsal abdominal glands of all nymphal instars were relatively well developed. These glands were elongate translucent swollen sacs, with some orange pigmentation. Scanning electron micrography showed the presence of a polygonal pattern of cuticular microsculpturing associated with the ostioles of dorsal abdominal glands (Figure 3).

## DISCUSSION

The most prevalent compounds found in *C. californicus*,  $\beta$ -myrcene and  $\beta$ -caryophyllene, are terpenoids commonly found in higher plants. These compounds are known from several species of *Croton* (Neto et al., 1994; Menut et al., 1995). The function of  $\beta$ -myrcene and  $\beta$ -caryophyllene in *C. californicus* is not known, although they are present in the defensive secretions of some Heteroptera (Gough et al., 1985; Krall et al., 1997). *Pachycoris stallii* may use the relative ratios of these compounds to differentiate between structures on which to feed (fruit) and those for oviposition (leaves). The ratio of  $\beta$ -myrcene to  $\beta$ -caryophyllene in *C. californicus* fruit is 2.5:1, while in leaves it is 1.5:1. It is also possible that *P. stallii* uses other plant characteristics, such as minor chemical constituents or physical factors (e.g., shape and texture of plant structures), to recognize different plant structures. The presence of *n*-tridecane in fruit and leaves is probably the result of degradation of hydrocarbon components of cuticular waxes (Goodwin and Mercer, 1986).

Results of chemical analyses demonstrated that *P. stallii* employs a carbonyl-based scent gland chemistry [C<sub>6</sub> alkenal (*E*)-2-hexenal, the C<sub>6</sub> 4-oxo-

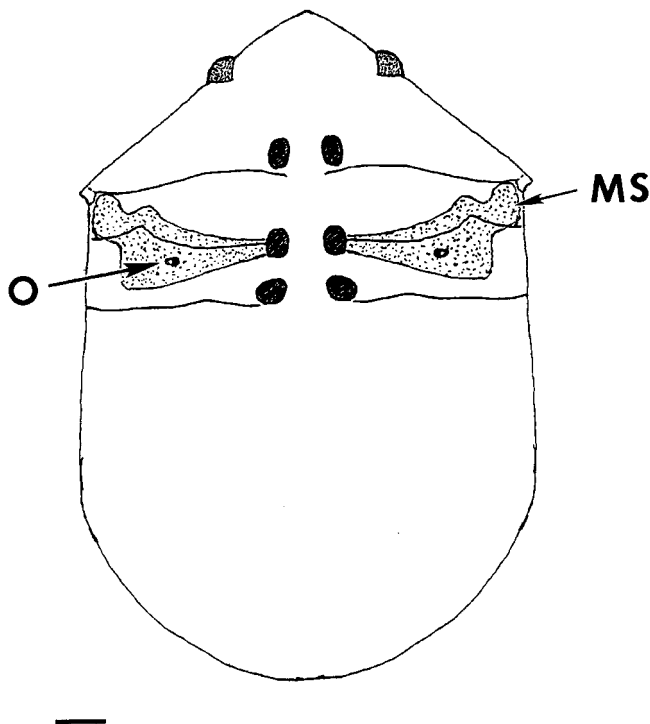


FIG. 1. Ventral view of *Pachycoris stallii* female showing the position of ostia (O) and microsculpturing (MS) on mesepisternum and metepisternum; scale bar = 1 mm.

2-alkenal (*E*)-4-oxo-2-hexenal, and the  $C_{13}$  alkane *n*-tridecane], which conforms to the general pattern for other Pentotomoidea (Staddon, 1979; Aldrich, 1988, 1995). As expected, the corresponding ester of (*E*)-2-hexenal, (*E*)-2-hexenyl acetate, was also present (Aldrich, 1988). Dorsal abdominal glands in adults were apparently obsolescent, while those of nymphs produced (*E*)-2-hexenal, (*E*)-4-oxo-2-hexenal, *n*-dodecane, *n*-tridecane, and the  $C_{14}$  alkanal tetradecanal. With the exception of tetradecanal, these compounds are typical of those found in dorsal abdominal glands of Pentotomoidea. Anatomical data indicate that defensive secretions are produced in well-developed metathoracic or dorsal abdominal glands, and field observations indicated that the allomones are delivered via an efferent system that allows the concoction to be squirted (Williams, unpublished observations). Light and electron microscopy revealed the presence of microsculptured cuticle surrounding the ostia of these glands, presumably to aid in the accumulation and evaporation of the secretion (Staddon, 1979).

Current evidence on the cytological sources of the compounds produced

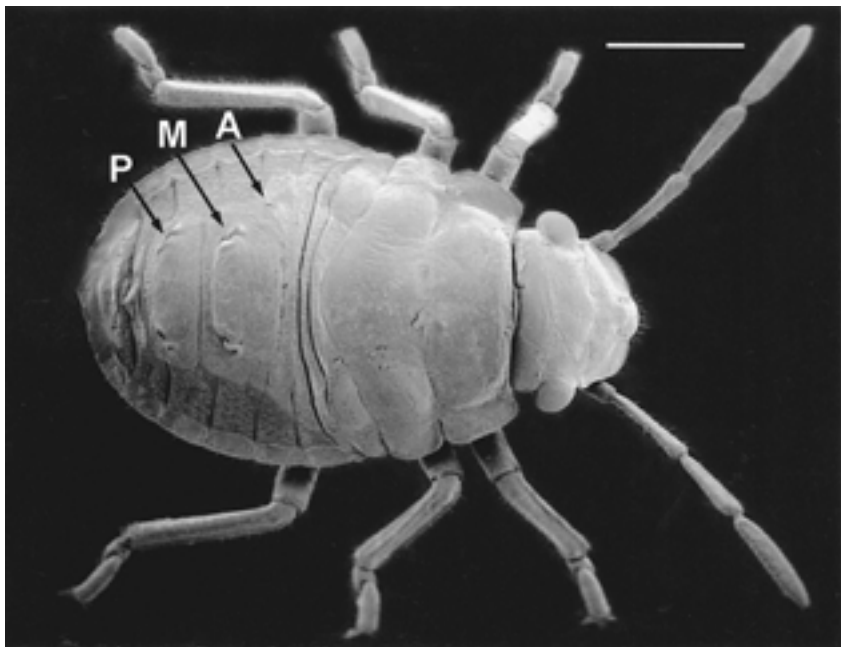


FIG. 2. Scanning electron micrograph of second-instar *Pachycoris stallii* showing arrangement of anterior (A), median (M), and posterior (P) dorsal abdominal gland ostia; scale bar = 1 mm, magnification 18 $\times$ .

in the metathoracic glands indicates that esters are synthesized in the secretory tubules, and alkanals and related scent carbonyls are generally restricted to the median reservoir (Gilby and Waterhouse, 1967; Aldrich et al., 1978; Everton et al., 1979). Results of the present study conflicted somewhat with this trend. Analyses from dissected metathoracic glands suggest that (*E*)-2-hexenyl acetate is secreted in MR/AG, after which it is converted to (*E*)-2-hexenal, and possibly to (*E*)-4-oxo-2-hexenal, as in other Heteroptera (Staddon, 1979). Small quantities of esters produced in secretory tubules are usually found in the median reservoir (Staddon, 1979), but this does not explain the absence of the ester in the LR/ST extracts in *P. stallii*. It is possible that the bugs from which extracts were prepared had, upon being agitated prior to dissection, used all available (*E*)-2-hexenyl acetate to produce (*E*)-2-hexenal. As expected, (*E*)-2-hexenal was found in extracts of female MR/AG, but was also detected in extracts of LR/ST. This suggests that in *P. stallii* (*E*)-2-hexenal is formed in the lateral reservoir as well as the median reservoir. In male bugs, *n*-tridecane was present in extracts of MR/AG, as expected, but also in extracts of LR/ST, suggesting that *P. stallii* is

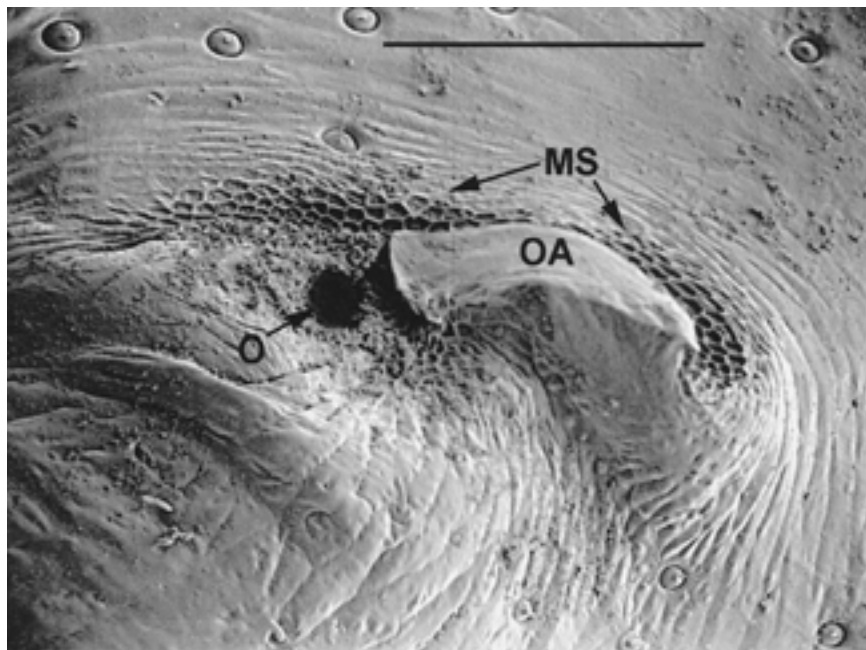


FIG. 3. Scanning electron micrograph of median dorsal abdominal gland of second instar *Pachycoris stallii* showing microsculpturing (MS), ostiole (O), and occlusion arm (OA); scale bar = 0.1 mm, magnification 416 $\times$ .

capable of producing *n*-tridecane in the secretory tubules and lateral and median reservoirs. Gilby and Waterhouse (1967) detected *n*-tridecane in the secretory tubules of *Nezara viridula* (L.).

Attributing biological significance to the differences between the chemical composition of allomones produced by *P. stallii* adults and nymphs is difficult in the absence of behavioral data. It is possible that the differences are not of great importance, as long as the chemical and physical characteristics of the mixtures result in an effective defense (Tschinkel, 1975). If this is true for *P. stallii*, then the differences may reflect different metabolic costs of synthesis between adults and nymphs. The differences observed may also reflect differences in natural enemies between nymphs and adults (Pasteels et al., 1982). Pasteels et al. (1983) suggested that such differences in composition might be a strategy to avoid counteradaptation by natural enemies. The above explanations may also apply to the observed changes in chemical composition of dorsal abdominal gland secretions between nymphal instars. Behavioral studies under field conditions will help elucidate the roles of scent gland secretions in different life stages of *P. stallii*.

Field observations supported the theoretical prediction that insects will utilize defensive secretions in a frugal manner and may use other defensive ploys before discharging allomones (Wallace and Blum, 1969; Whitman et al., 1990). The first line of defense for *P. stallii* is to run down stems away from the aggressor or drop to the leaf litter under the plant canopy (Williams, unpublished observations). Brooding females remain with their young and use behavioral defenses, such as kicking, towards an aggressor. These females were rarely induced to eject defensive secretions, possibly to avoid poisoning their offspring. Usually, bugs were induced to discharge allomones only after considerable physical contact, such as being pinched with forceps or after being handled. When bugs did discharge gland contents, they demonstrated the ability to squirt them toward an aggressor from a single ostiole, further suggesting that *P. stallii* uses allomones in a conservative manner.

The chemical nature of the scent glands of *P. stallii* suggests that this defensive system is directed at arthropods. The aliphatic aldehydes [e.g., (*E*)-2-hexenal], ketoaldehyde [(*E*)-4-oxo-2-hexenal], and *n*-alkanes (e.g., *n*-tridecane) produced by *P. stallii* are nonspecific irritants, toxins, or olfactory repellents of arthropods (Blum, 1981; Pasteels et al., 1983). Moreover, *n*-tridecane is believed to act as a surfactant and evaporatory retardant, as well as aid in the penetration of toxic aldehydes through an aggressor's cuticle (Staddon, 1979; Gunawardena and Herath, 1991). The nonspecific volatiles produced by *P. stallii* are known to deter ants (Blum, 1961; Wallace and Blum, 1969), and may also mimic alarm pheromones of ants, allowing bugs to escape (Blum, 1980). In the present study, field observations suggested that ants were the primary arthropod predators of *P. stallii*. *Dorymyrmex bicolor* Wheeler was commonly observed patrolling stems and leaves of *C. californicus*, as well as the soil surface, where they attacked nymphs and adults that fell to the soil and were immobilized by high surface temperatures. The ants were sometimes successful in driving brooding female bugs away from egg masses, after which eggs were consumed. Our results suggest that *P. stallii* is an aposematic heteropteran that, despite feeding on a host plant toxic to vertebrates, has maintained a potent exocrine defense system directed at arthropod predators.

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